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Status of *Miconia calvescens* (Melastomataceae), a Dominant Invasive Tree in the Society Islands (French Polynesia)[1]

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ABSTRACT: Since its introduction to Tahiti in 1937 as an ornamental, *Miconia calvescens* DC. (Melastomataceae) has become the most important plant pest in the Society Islands. Its ecological characteristics allow it to thrive and spread in a wide range of habitats, including native forest, where it forms dense monotypic stands. *Miconia calvescens* now dominates over two-thirds of Tahiti and has spread to the surrounding islands of Moorea and Raiatea. This species represents an immediate threat to the native flora of all the high islands of French Polynesia and a potential danger to many tropical oceanic islands.

NUMEROUS CASES OF biological invasions have been described in native vegetation of oceanic islands, including the Hawaiian Islands (Smith 1985, Stone et al. 1992), Galápagos Islands (Schofield 1989), Guam (Lee 1974), Mauritius (Lorence and Sussman 1986), and La Réunion (Macdonald et al. 1991). High susceptibility of island ecosystems to invasion may be largely the result of relative impoverishment of flora and fauna (low species number, taxonomic disharmony) and of evolution in long isolation from outside influences (Loope and Mueller-Dombois 1989). Another factor in many instances is that aggressive invaders have been introduced without the specific natural predators that have evolved in their native range.

The case of *Miconia calvescens* De Candolle in Tahiti provides an extremely dramatic example of the effect of a single invasive species on the biological diversity of an oceanic island. Introduced to Tahiti as a garden ornamental in 1937, it has spread to form monotypic stands, replacing former native forest, and now dominates the forest over 65% (ca. 70,000 ha) of the island.

This paper is an attempt to synthesize what is known about the introduction, spread, distribution, and effects of *M. calvescens* in the Society Islands, as well as some of the biological characteristics that contribute to the success of this invasive tree and make it a potential danger to the forest of many moist, tropical oceanic islands.

Study Area

The Society Islands, the largest group of high islands in French Polynesia, form one of the most isolated archipelagoes in the world, lying at 15–18°S, 148–154°W in the South Pacific Ocean, 5000–6000 km from the nearest continents. They include nine high islands (Bora Bora, Huahine, Maiao, Maupiti, Mehetia, Moorea, Raiatea, Tahaa, and Tahiti) of volcanic origin, less than 4.5 myr old, and five coral atolls (Manuae, Maupihaa, Motu One, Tetiaroa, and Tupai). The archipelago is divided into the Windward Group and the Leeward Group based on the position of the islands relative to the dominant southeast trade winds (Figure 1). The climate is tropical oceanic with two seasons: a warm and humid season with torrential rains from December to February and a cooler, drier season from March to November; mean annual temperature is 26°C (absolute maximum 34°C in January, absolute minimum 15°C in August); relative humidity ranges from 76 to 80%; annual rainfall averages 1700 mm/yr at sea level (Pasturel 1993). Precipitation increases rapidly orographically more on wind-

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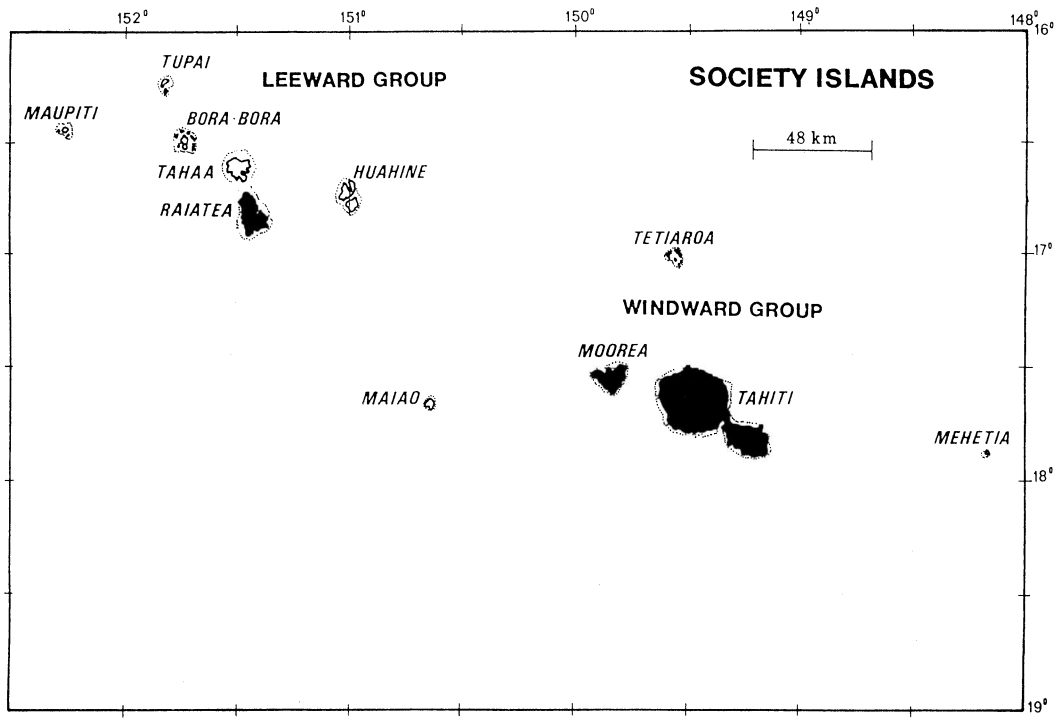

FIGURE 1. Distribution of *Miconia calvescens* in the Society Islands of French Polynesia (invaded islands are shown in black).

ward sides (sometimes up to 10,000 mm/yr) than on leeward sides.

Floristic richness of islands in the tropical Pacific depends on their physiographic and ecological diversity. The Society Islands, with their high, complex islands, have 623 native species (including 273 endemics) of the 959 vascular plant species native to French Polynesia (Florence 1987). Colonizing Polynesians brought with them, 2000–2500 yr ago, an additional 80 plant species (J. Florence, pers. comm.) and several animal species. Over 1500 introduced plant species have been collected by J. Florence in the Society Islands (pers. comm.). They were introduced either intentionally (for agricultural, construction, medicinal, or ornamental use) or inadvertently since European contact in the eighteenth century. Many of them are naturalized, and some, such as *Cyperus rotundus* L. (Cyperaceae), *Lantana camara* L. (Verbenaceae), *Melinis minutiflora* P. Beauv. (Poaceae), *Merremia peltata* (L.) Merril (Convolvulaceae), *Mimosa invisa* Martius ex Colla (Fabaceae), *Psidium guajava* L. and *Psidium cattleianum* Sabine (Myrtaceae), and *Rubus rosifolius* Sm. (Rosaceae) have become locally dominant in secondary vegetation and are considered as "plant pests." *Miconia calvescens*, although also a pest in disturbed sites, is unique in its extension in apparently undisturbed native ecosystems and its efficiency in eliminating other species.

Description of the Study Species

In the Society Islands, *Miconia calvescens* (Melastomataceae: Miconieae) is a small tree up to 15 m high. Most often, mature trees are between 6 and 12 m tall, with slender, stiff vertical stems. Because of its large, dark green, handsome leaves (up to 1 m long), which have three prominent, pale green nerves above and are more or less purple-blue underneath (Figure 2), *M. calvescens* (also called *M.*

FIGURE 2. Because of its large, attractive leaves, more or less purple underneath, *Miconia calvescens* is cultivated in European greenhouses and tropical botanic gardens and is still considered one of the most magnificent foliage plants (Graf 1986).

magnifica Triana in horticulture) was introduced to European botanical gardens and cultivated in greenhouses for its ornamental value (Wurdack 1971) . It was then considered as "one of the best and most striking of all conservatory foliage subjects" (Bailey 1900 : 1012).

The leaves are opposite, elliptic to obovate, entire or undulate, rounded or subcordate at the base, shortly acuminate or sometimes obtuse to rounded at the apex with a 4- to 10-cm-long petiole, glabrous above, and puberulous with minute stellate hairs underneath. Flowers are small, white, more or less sessile, bisexual, 5-merous, and slightly fragrant, arranged in large panicles. Younger branches and base of the panicle are also thinly cinereous with minute stellate hairs.

Natural Distribution

To check the native range of *M. calvescens*, I observed the specimens available in some major herbaria (Royal Botanical Garden of Kew [K], Museum national d'Histoire naturelle de Paris [P], Institut für Botanik der Universität Wien [WU], U.S. National Arboretum of Washington [NA], Bishop Museum of Honolulu [BISH]). I collected other information from V. Sosa (Instituto de Ecología, A. C., Mexico), M. G. Peña (Herbario Nacional de Mexico, Mexico), S. C. Chiea (Instituto de Botanica, Brazil), F. Almeda (California Academy of Sciences, USA), and R. Burkhart (State Department of Agriculture, Hawai'i, USA). The identification of most herbarium specimens was checked by J. J. Wurdack.

The native range of *M. calvescens* extends over more than 40° of latitude, from about 18°N in southern Mexico to about 26°S in southern Brazil and northern Argentina (Figure 3). Specimens of the bicolorous form with purple leaf undersides have only been collected in southern Mexico (Chiapas, Oaxaca), northern Guatemala, Belize, and Costa Rica.

Information on herbarium labels suggests that the species is found from lowland to montane tropical forest (up to 1800 m in Ecuador [Wurdack 1980]), sometimes in dense shade of primary forest, but most often in more open vegetation (old pastures, forest edges, river banks, trailsides and roadsides, disturbed areas). Like most of the 1000 other species of the genus *Miconia*, *M. calvescens* seems to be a shade-tolerant understory tree that behaves like a pioneer tree in forest gaps. In its native range, this species "is never common at any one site" (F. Almeda, pers. comm.).

Ecology and Dispersal

Many of the biological characteristics of *M. calvescens* make it a potential pest outside its native range. It is a fast-growing tree (up to 1 m/yr for juvenile plants under optimum conditions [Meyer 1994]) that can flower and fruit after 4–5 yr from seed. There are at least three peaks of flowering and fruiting per year

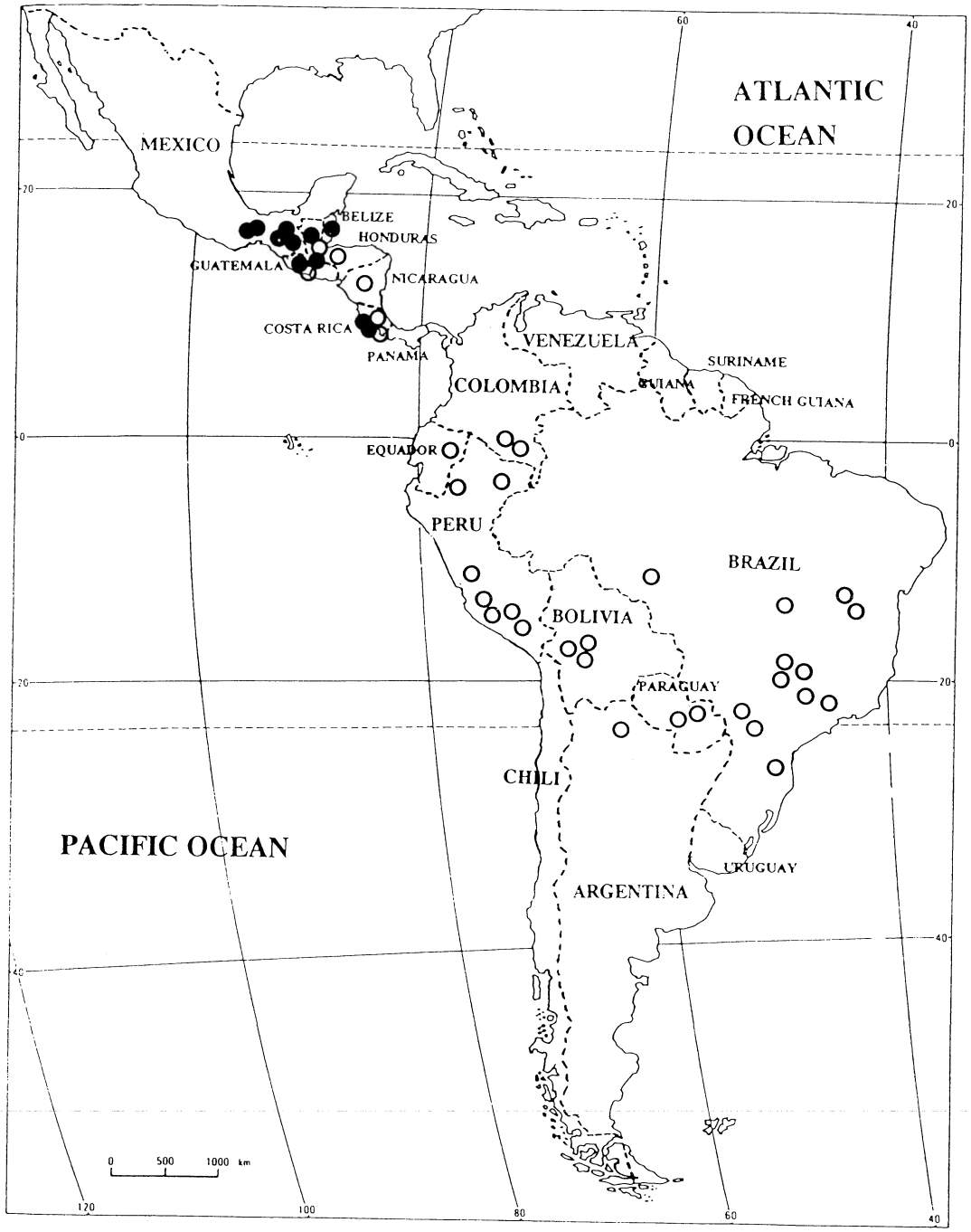

FIGURE 3. Native range of *Miconia calvescens* according to herbarium specimens. Bicolorous form is indicated by closed circles and form with green leaves by open circles.

within populations (Meyer 1994), but with some inter- and intraindividual variability (Gaubert 1992). Panicles of fleshy berries (up to 500 fruits per panicle) are produced, with each fruit 0.6–0.7 cm in diameter, blue-black when ripe, containing an average of 140–230 seeds, each ca. 0.7 by 0.5 mm long (Meyer 1994). With two panicles typical for the first season of production, a young fruiting tree produces ca. 200,000 seeds in its first season. A large fruiting tree with over 50 panicles can produce over 5 million seeds a year. In the field, the large size of the soil seed bank (>50,000 seeds per m^2 in the most invaded area of Tahiti [Gaubert 1992]) and its longevity (>2 yr in soil samples [Meyer 1994]) give *M. calvescens* a formidable reservoir of regenerative capacity even if all plants are removed from an area. In the laboratory, some seeds germinate rapidly (15–20 days) when exposed to light and moisture, but others remain dormant for up to 6 months; over 90% eventually germinate under optimal conditions. Germination occurs even in dense shade (at 0.02% of full sun [Meyer 1994]) and on poor substrate (on rocks or barks of trees). Vegetative layering and resprouting also occur.

Ecosystems become completely transformed in species composition as *M. calvescens* gains dominance. Proliferation of the broad leaves and overlapping architecture of this species result in a dense shade that no native species can tolerate. Meanwhile, the superficial, tentacular root system of *M. calvescens* may not hold the soil well: *M. calvescens* dense stands are suspected of contributing to landslides in Tahiti (S.E.D.E.P. 1988).

Passive dispersal occurs by gravity (most fruits fall beneath the trees), wind (seeds are minute and light), and water (seeds germinated from fruits I had left for 3 months in water). Frugivorous birds have been observed in Tahiti feeding on *Miconia* fruits. Among them, two introduced birds, the Silvereye (*Zosterops lateralis* Latham) and the Red-vented Bulbul (*Pycnonotus cafer*), are believed to be important dispersers (Gaubert 1992). Introduced to Tahiti in 1937, the Silvereye has since become the most abundant terrestrial bird, occupying all ecological habitats on the island. The Red-vented Bulbul, first noticed in Tahiti in 1979, has become abundant in the coastal and lowland zones. Small rodents may play an important role in *Miconia* seed dispersal: I have found numerous viable seeds in droppings of the quite abundant and frugivorous Polynesian rat, *Rattus exulans* Peale (Meyer 1994). Finally, both intentional and unintentional actions by humans are believed to be important in the short- and long-distance transport of *M. calvescens*. Seeds are undoubtedly picked up with mud and carried on shoes and vehicle wheels. They are known to have been carried with the soil of potted cultivated plants (see below).

Introduction and Distribution in the Society Islands

TAHITI. Tahiti, the largest (1045 km^2) and highest (2241 m) island in the Society Archipelago, is formed from two distinct ancient volcanoes, Tahiti Nui ("large," 30 km in diameter) and Tahiti Iti ("small," 22 km by 13 km), connected by the low and narrow isthmus of Taravao (Figure 4).

M. calvescens was introduced in the private botanical garden of Motu Ovini (now called Papeari Botanical Garden), on the southwestern coast of Tahiti, in 1937 by Harrison Willard Smith, a retired American physics professor and exotic plant fancier. The original label of the plant can still be seen at the botanical garden. Smith obtained seeds of *M. calvescens* from the Royal Botanic Gardens of Peradeniya in Sri Lanka (then Ceylon), where it had been introduced from Mexico in 1888 (A. H. M. Jayasuriya, pers. comm.). *M. calvescens* was apparently planted later (date unknown) on the grounds of the Agriculture Research Station at Taravao by Jean Boubée (Raynal 1979), a French agronomical engineer who was a colleague and friend of Harrison Smith.

There are no records of the spread of *M. calvescens* in Tahiti until the 1970s. In 1971, botanist F. R. Fosberg of the Smithsonian Institution of Washington, D.C., saw this species and was dismayed by its invasiveness.

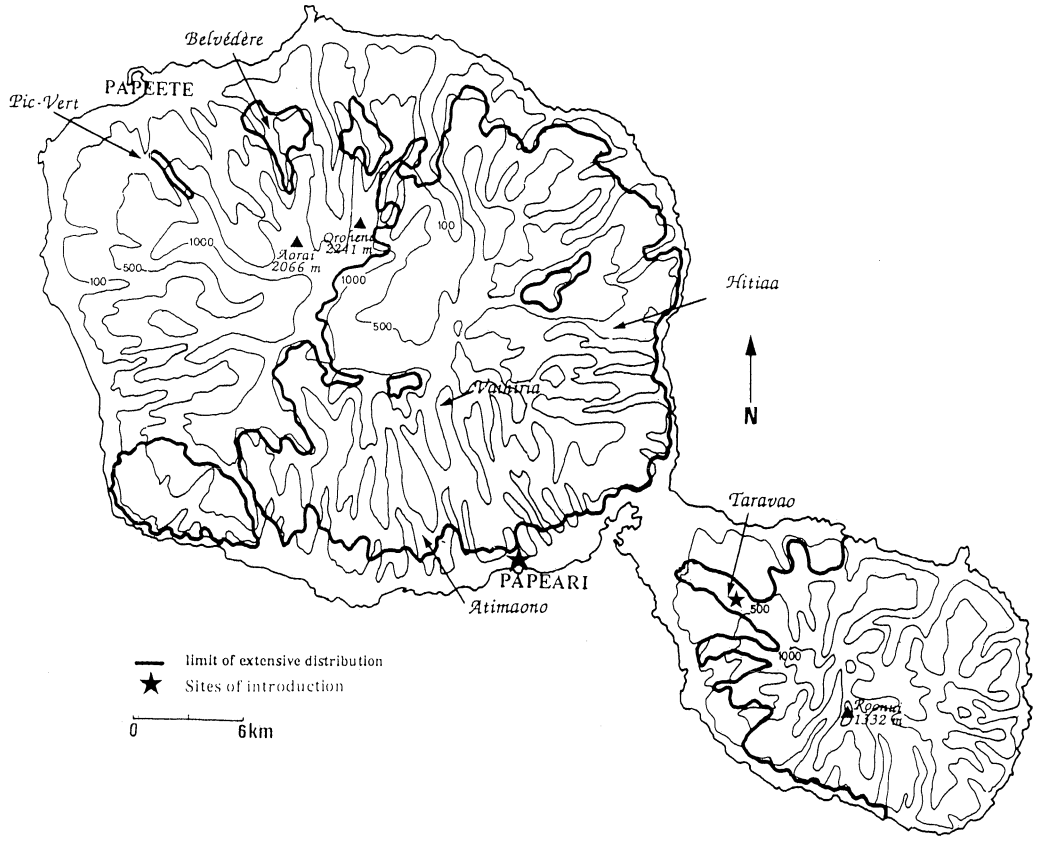

FIGURE 4. Distribution of *Miconia calvescens* on the island of Tahiti (after Birnbaum 1991).

He warned authorities in Hawai'i to prohibit its introduction there (Loope and Medeiros 1994). Botanist Jean Raynal of the Museum national d'Histoire naturelle of Paris proclaimed *M. calvescens* the "number one enemy of Tahitian vegetation" (Raynal 1973: 11), after noting that it already formed pure stands on the top of the plateau above Taravao and that it had been reported at 600–650 m elevation at the Belvédère above Papeete, more than 30 km from the nearest known site of introduction. Whether *M. calvescens* was planted as an ornamental at the Belvédère or whether it had already expanded across the island is unknown. In 1976, ethnobotanist M. A. Martin found some individuals in the lower part of the Papenoo Valley and wrote that "*M. calvescens* would be more frequent higher in the valley" (Martin 1976: 5).

An analysis of 1978 aerial photographs taken on the plateau of Taravao showed that only an area of 100–200 ha of *M. calvescens* was visible in the forest canopy (Birnbaum 1991). However, this is an underestimate of the real spread of this plant pest, which was also present in canopy and understory in other valleys of Tahiti Iti, but not noticeable on aerial photographs (J. Florence, pers. comm.). Furthermore, Raynal (1979: 149) noted that "there are pure stands from Taravao to the Vaitepiha, the main valley of Tahiti Iti." In 1979, professor of biology B. Le Vot noted that *M. calvescens* had invaded the totality of Tahiti Iti south of Tahiti Nui and entered into the caldera (Le Vot 1979). In 1981, *M. calvescens* had "supplanted all other vegetation on certain slopes on the south side of the island, is spreading everywhere in the moist

valleys, and is proving to be serious competition for the native vegetation" (Fosberg and Sachet 1981 : 36). During an expedition to Lake Vaihiria in May 1982, Jacques Florence (1982 : 3–4), botanist of the Centre ORSTOM de Tahiti, noted that "the presence of *Miconia* is particularly impressive on the sides of the lake where it has already invaded the *Cyathea-Pandanus* forest and makes the landscape look like a biological desert." It has been suggested that a dramatic increase of *Miconia* followed the cyclones of December 1982 and April 1983 (Birnbaum 1991), but no conclusive evidence is available. It is more likely that *M. calvescens* was already present in the understory and that canopy openings caused by the cyclones favored growth and flowering (J. Florence, pers. comm.). Colonization of new open areas created by treefalls and landslides seems less likely.

In less than 50 yr since its introduction, *M. calvescens* has spread widely throughout much of the Tahitian forests, as shown by the distribution map made by P. Birnbaum in 1989 (Birnbaum 1991) (Figure 4).

MOOREA. Moorea is a small island (142 km^2) with steep relief: a large number of peaks, many between 700 and 900 m elevation, form a mountainous chain that encircles the Domaine d'Opunohu, a low-lying agricultural and forestry zone (Figure 5).

Two primary centers of establishment of *M. calvescens* are located on the summit and slopes of Mount Rotui (899 m) and Mount Mouaputa (860 m). Establishment of a small population was first noted in the early 1970s on Mount Mouaputa by an inhabitant of Afareiatu, the main village of the island (R. Shigetomi, pers. comm.). The remote mountaintop location of both the Mouaputa and

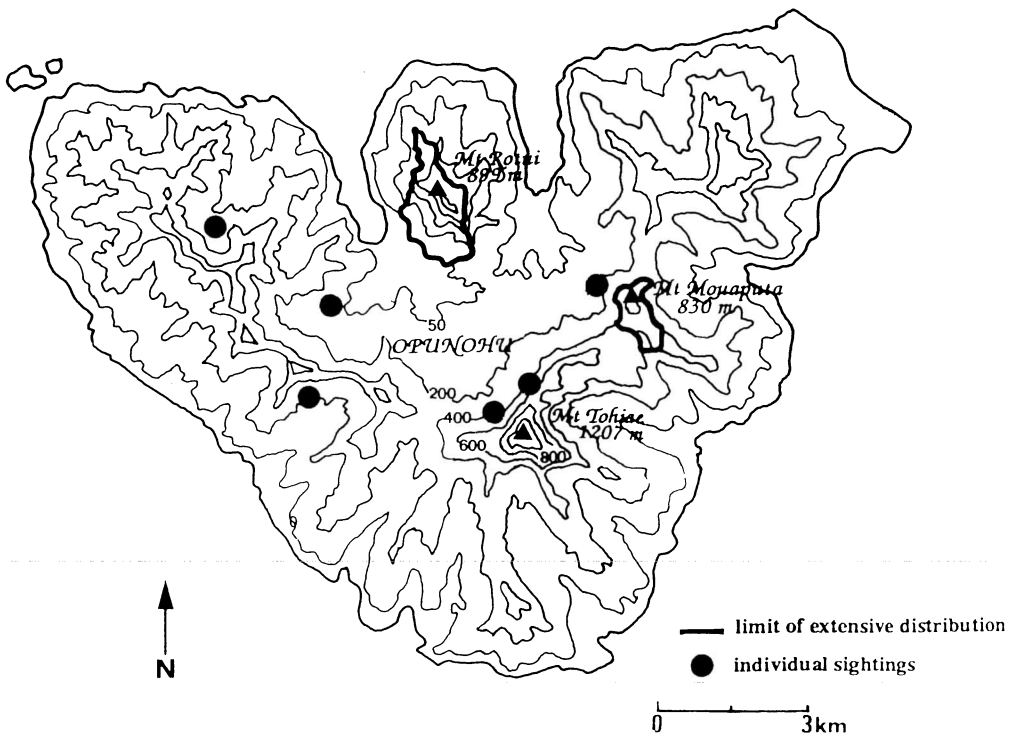

FIGURE 5. Distribution of *Miconia calvescens* on the island of Moorea.

Rotui populations suggests possible dispersal from Tahiti (only 18 km distant) by wind, birds, or recreational hikers. Currently, occurrences ranging from individual trees to dense localized populations have been reported in many locations within and on steep slopes above the Domaine d'Opunohu (Schwartz 1994).

RAIATEA. Raiatea, the largest (171 km^2) of the Leeward Islands, is located 180 km WNW of Tahiti. Unlike Moorea, Raiatea has relatively smooth relief dominated by the two plateaus of Temehani at 500–800 m elevation (Figure 6).

Small populations of *M. calvescens* covering a total of ca. 240 ha were reported in

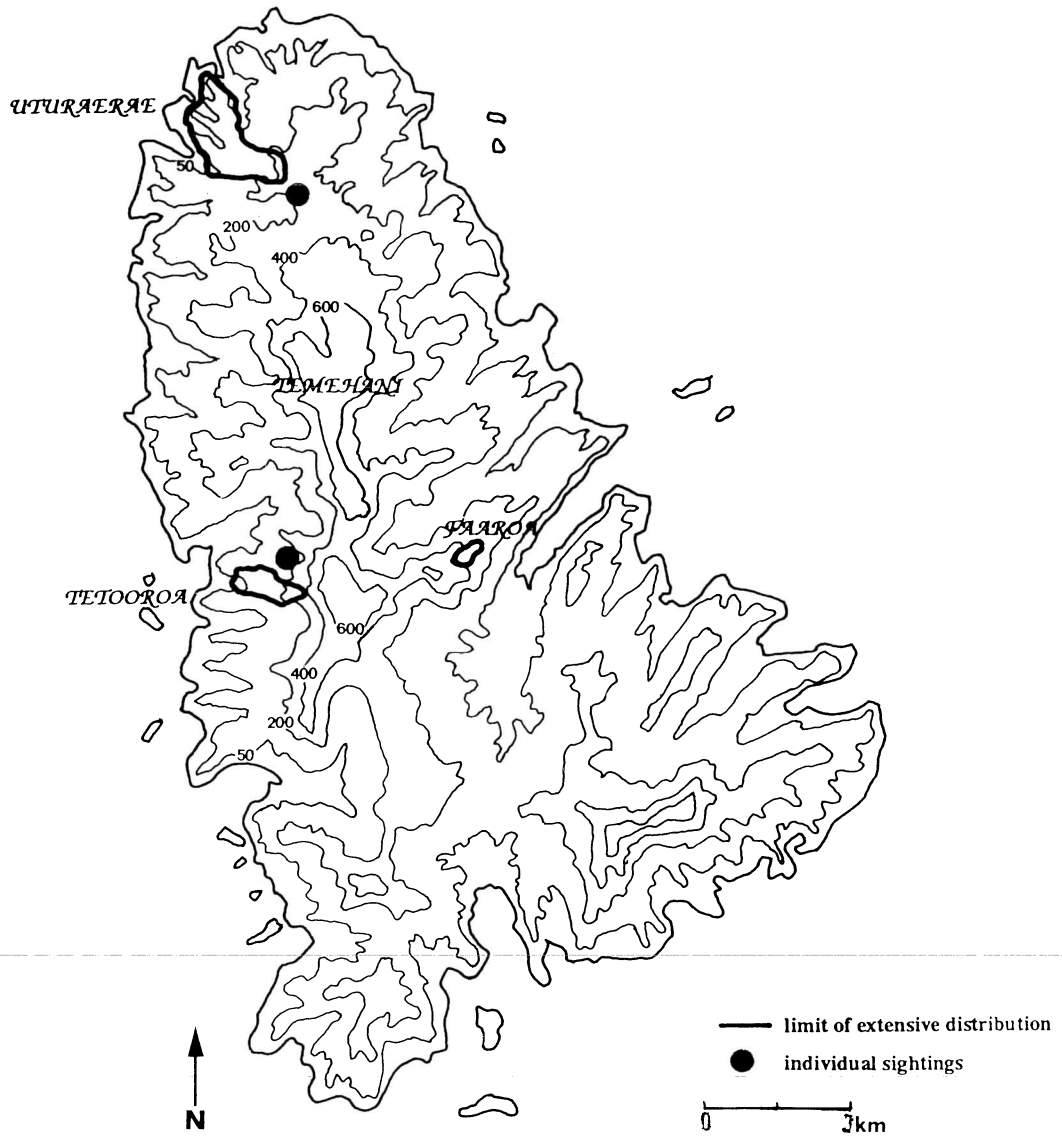

FIGURE 6. Distribution of *Miconia calvescens* on the island of Raiatea.

three separate valleys (Uturaerae, Tetooroa, and Faaroa) in 1988 by the forestry section of the Service de l'Economie Rurale (J.-P. Malet, pers. comm.). The Uturaerae population originated from an ornamental planting in 1955 that had become naturalized by 1969–1970 (R. Amiot, pers. comm.); by 1989, there were dense, monotypic stands in the valley bottom (Florence and Birnbaum 1989). In the moist (mean annual rainfall >5000 mm/yr) valley of Tetooroa, seeds of *M. calvescens* are believed to have been introduced with soil of coffee plants from Tahiti in the 1970s. Introduction of the Faaroa Valley population probably dates back to 1981 with the beginning of the forestry industry (*Swietenia macrophylla* King plantations) and the introduction of "contaminated soil" from Tahiti (Malet 1992).

Dispersal from the three Raiatea populations of *M. calvescens* has been limited largely by surrounding plantations of pine forest on ridgetops. This fortuitous circumstance has allowed promising control efforts by the forestry section of the Service de l'Economie Rurale. A total of ca. 25,000 plants (including 500 large, seed-producing trees) was hand-removed in June 1992, with assistance of 200 school volunteers. Follow-up in June–July 1993, with the help of 100 soldiers from the French Army, removed more than 77,000 plants. Seedlings and saplings were uprooted, and trees too large to be uprooted were cut and stumps treated with herbicide (2,4-D) to prevent resprouting. Although follow-up will be necessary for several years to allow the exhaustion of the seed bank, there seems to be a good chance of eradicating *M. calvescens* from Raiatea.

CONCLUSIONS

Miconia calvescens has already attained dominance over most of the island of Tahiti. Dense, monotypic stands of this species occupy mesic and wet environments (mean annual rainfall >2000 mm) at 10–1300 m elevation. It not only occupies roadsides, forest edges, and abandoned pastures, but also has invaded primary native forests. It changes the light regime and is suspected of causing landslides; it alters, therefore, "the basic rules of existence of all organisms" (Vitousek 1990: 8). Its invasion of native forest is progressively eroding native biological diversity: half of all the endemic species of Tahiti are directly endangered by *M. calvescens* (J. Florence, pers. comm.). The success of *M. calvescens* in the Society Islands is apparently a result of the ecological characteristics of the species that allow it to thrive and spread (rapid growth rate under optimal conditions, prolific seed production, efficient dispersal, persistence in the soil seed bank, shade tolerance) under suitable environmental conditions; the absence in the Society Islands of the specific natural enemies that are present in its native range in Central and South America (R. Burkhart, pers. comm.), where the species is not abundant; and a presumed inherent vulnerability of island forests to invasion.

Because similar factors are present in high oceanic islands throughout the Tropics, the possibility of destructive invasion of other archipelagoes by *M. calvescens* is obvious. Stringent measures are needed to prevent the spread and escape of this aggressive species to other locations. The striking appearance of the plant, with its large green and purple leaves, makes it attractive to plant fanciers (Graf 1986).

Miconia calvescens recently was recognized as an unwelcome addition to the nearly 100 dangerously invasive plant species of the Hawaiian Islands (Smith 1985, Gagné et al. 1992); unfortunately, by the time serious control measures were instituted, it had been present for over 20 yr and spread to multiple loci on two islands (L. L. Loope and A. C. Medeiros, pers. comm.). It also occurs in such locations as the Philippines (R. Petocz, pers. comm.), Grenada (P. Cazin, pers. comm.), and New Caledonia (R. Lavoix, pers. comm.) as an ornamental, not yet naturalized.

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